# ENERGETICS

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## I. Introduction

Measurement of energy acquisition and allocation provides a quantitative assessment of how animals organize their daily or seasonal activities, and how they prioritize their behaviors to maximize fitness. What goes in as food and comes out as growth, reproduction, repair, waste, or metabolic work can be described by energy flow models (Fig. 1). At a minimum, survival requires that the individual breaks even in terms of energy costs and benefits, balancing the costs of self-maintenance versus energy acquired. To grow and reproduce, animals must obtain more energy than is needed to survive, so that they are in positive energy balance. Many marine mammals undergo variations in energy balance, gaining energy while feeding in highly productive environments, followed by fasting during migration or reproduction.

This balance between energy acquisition and expenditure, as well as the temporal and spatial scales across which it is achieved, differs markedly between species and environments. For some species, including sea otters, sea lions, and fur seals, high rates of energy expenditure are met by high rates of energy acquisition (Costa and Williams, 2000). These animals preferentially live in nearshore environments or upwelling regions where food is abundant (Costa, 1993), finding energy balance on smaller (10s to 100s of kilometers), more immediate (daily to weekly) scales (Williams and Maresh, 2016).

Other species, including seals and baleen whales, have low rates of energy expenditure, allowing them to alternate between high rates of energy acquisition and fasting. These animals achieve energy balance over larger spatial (100s to 1000s of kilometers) and time (months to years) scales. This strategy takes advantage of seasonally productive environments, building energy reserves that can be used when food is not available. Although maintenance costs may be elevated in polar regions, the seasonally high productivity associated with sea ice during the polar summer supports high-energy acquisition rates that more than compensate. As time passes and whales are confronted with the high costs of reproduction during a polar winter, they opt for the more thermally benign but energy-poor tropics. Spending time in the tropics also provides an opportunity to repair and "refurbish" their skin (Durban and Pitman, 2012).

As obligate herbivores, manatees and dugongs have adapted to a diet of seagrasses and other aquatic plants that are in high abundance but of low caloric value. Sirenians are able to offset low energy intake rates by living in tropical environment that keeps maintenance costs low while consuming a herbivorous diet that takes little energy to acquire. However, the thermal constraints of extant sirenians make one wonder how the Steller sea cow managed to survive in the cold waters of the Bering Sea on a diet of kelp (Estes et al., 2016).

While the best situation is to have access to abundant, high-energy prey, in some scenarios low-quality prey that is more abundant and nearby may be more optimal than searching for high-quality prey that is difficult to find. As prey becomes less available, the cost of finding it increases and the animal spends a greater proportion of its time and therefore energy searching for it. Eventually, there is a threshold beyond which more energy is spent searching for prey than is obtained and the animal goes into negative energy balance (Villegas-Amtmann et al., 2015).

## II. Energy Acquisition

Animals are not able to extract all of the chemical energy available in ingested prey (IE) (Fig. 1). Some of the material consumed is not digestible, and will be lost as feces (FE), with the remaining food energy known as the apparently digested energy (ADE). Assimilation efficiency ranges from 88% to 98% for a diet of fish, to 72% for invertebrate prey with a high chitin content (Costa and Williams, 2000). Assimilation efficiency is highest on a high lipid diet (Diaz Gomez et al. 2015) or when a diverse diet with different

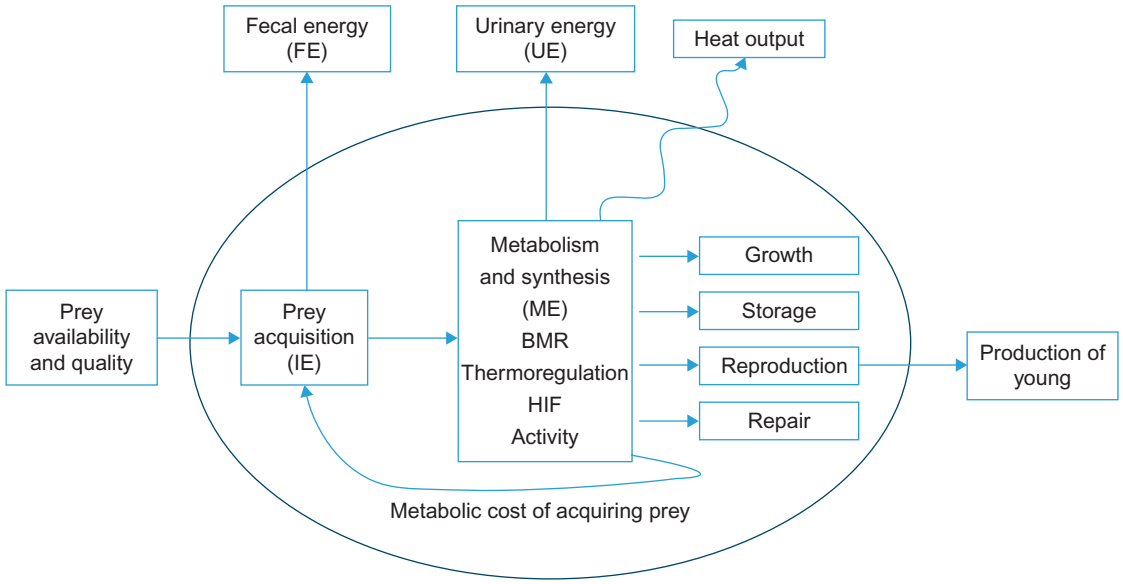


**Figure 1** *A conceptual diagram of energy flow through a typical mammal. The outer oval represents the animal. Anything that passes through that envelope is material (straight line) or energy (waved line) entering or leaving the animal. IE, ingested energy; ME, metabolic energy; FE, fecal energy; and UE, urinary energy.*

proximate compositions is consumed (Trumble and Castellini, 2005). Due to its high cellulose content, plant material is harder to digest and thus sirenians extract only about 85% of IE, but this is higher than terrestrial hindgut fermenters, such as horses (45%–59%).

## III. Energy Expenditure

### A. Maintenance Costs

1. *Basal metabolism*: Measurements of the basal metabolic rates (BMR) of aquatic mammals have been complicated as many studies did not conform to standardized criteria for BMR measurements, which requires that subjects be adults, resting, thermoneutral, nonreproductive, and postabsorptive. As these criteria were developed for terrestrial mammals, it is unclear how comparable measurements are for marine mammals that are taken when the animals are swimming and diving. This has been further confused by the expectation that all marine mammals are physiologically similar. Specialization for marine living has occurred independently in three mammalian orders: the sirenians, cetaceans, and carnivores, and we see different metabolic adaptations between the groups (Fig. 2). Sirenians have BMRs lower than predicted values, phocid seals are closer to predicted, and sea otters, otariids, and odontocetes appear to have BMRs greater than terrestrial mammals.

   BMR varies with diet. For example, all carnivorous marine mammals, regardless of their ancestry, have longer small intestines than similarly sized terrestrial carnivores. The high metabolic costs associated with the maintenance of these digestive organs may enable the processing of large quantities of prey (Williams et al., 2001), which makes possible the high reproductive rates of cetaceans and pinnipeds (Sibly and Brown, 2007). These high metabolic rates can only be sustained in an environment where high-quality prey are abundant and available.

   BMR varies seasonally, with the animal's nutritional state, and with body composition. For example, sirenians and walrus, *Odobenus rosmarus*, have dense bone, whereas phocid seals may be composed of as much as 50% fat. A disproportionate amount of fat or dense bone will lower the BMR due to the low metabolic rates of these tissues in comparison to lean tissue. This effect is seen within individuals as well, as many marine mammals undergo prolonged fasts that are accompanied by profound changes in body composition. For example, northern elephant seal females lose 42% of their initial mass during lactation, with only 15% coming from lean tissue. Since lean mass is the primary contributor to whole animal metabolism, the animal's total metabolism changes little even though there has been a major change in its body mass and mass-specific metabolism.
2. *Heat increment of feeding*: When food is consumed, the animal's metabolic rate increases over fasting levels. The HIF, also known as the specific dynamic action (SDA), is the digestive "tax" required to convert food energy to metabolizable energy (ME), and varies between 5% and 17% of ME (Costa and Kooyman, 1984; Rosen and Trites, 2015). HIF is often considered waste heat; however, sea otters incorporate this heat to meet the high thermoregulatory costs associated with their small size (Costa and Kooyman, 1984). While grooming, feeding, and swimming sea otters use the heat produced from activity to supplement their thermoregulatory needs, at rest they incorporate the heat produced from HIF (Fig. 3). In diving animals, the HIF causes an increase in metabolic costs, which can be deferred to when the animal is at the surface (Rosen et al., 2015) or to dives that are explicitly for digestion (Crocker et al., 1997).
3. *Thermoregulation: Fur Versus Blubber*: There are differences in the energy budgets of animals that use fur or blubber for insulation. Although fur is not a living tissue, it requires maintenance of an air layer, which is done by frequent grooming. In contrast, while sea lions, seals, cetaceans and sirenians spend no time grooming,

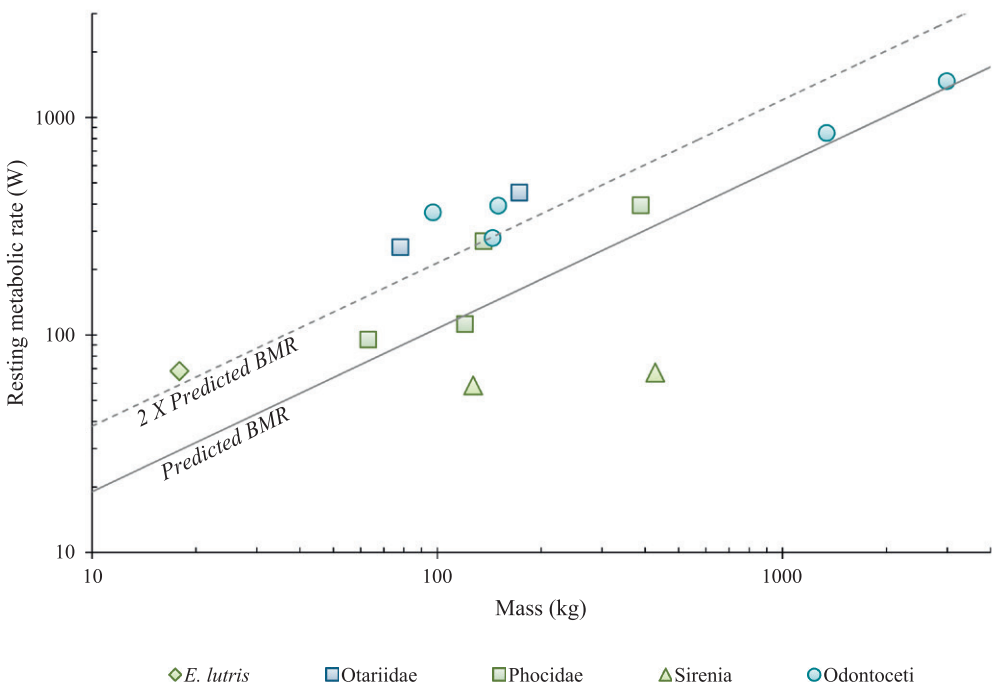


**Figure 2** *Resting metabolic rate (RMR) of marine mammals in relation to body mass. Measurements were made for animals resting in water. The solid line denotes the predicted basal metabolic rate (BMR) for equally sized terrestrial mammals; the dashed line represents two times the predicted BMR.*

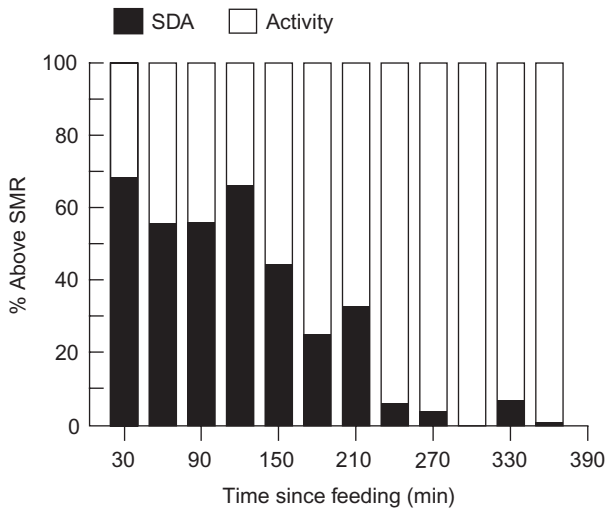


**Figure 3** *The thermal budget of sea otters relies on heat production above SMR. As HIF decreases the animal becomes more active and thus compensates for the decrease in heat production from HIF (Costa and Kooyman, 1984).*

**Figure 4** *California sea lions,* Zalophus californianus, *huddling—a behavior typical during cold mornings and winter months (Photo by Dan Costa).*

they must take in sufficient food to maintain a blubber layer, which is a living tissue and must be supplied with blood. Blubber serves roles as both an insulator and an energy store, thus requiring a balance between these competing needs. For pinnipeds in cold climates, an inexpensive way of increasing blood flow to the skin while ashore is to huddle together, effectively reducing their surface area that is exposed to the cold (Fig. 4).

## B. Locomotion and Foraging Costs

1. *Energetics of locomotion*: Marine mammals utilize strategies to keep locomotory costs low during long-distance migrations and while diving. In mysticete whales, for example, total costs during migration may not be elevated above maintenance levels since its travel speed is nearly identical to the speed at which the cost of transport is minimum. While diving, marine mammals can reduce costs by utilizing unsteady swimming strategies. As the biomechanical work to power each flipper, fluke or paw stroke requires some amount of metabolic power (energy), marine mammals periodically "turn off the motor," providing an energetic advantage over continuous stroking (Williams and Maresh, 2016). The interaction between body condition and hydrostatic pressure allows diving animals to take advantage of natural changes in buoyancy with depth to passively sink or ascend during different portions of the dive.
2. *Energetics of foraging behavior*: Most marine mammals are active predators, and thus foraging represents a major component of energy expenditure through costs associated with prey capture; however, different foraging behaviors are associated with different metabolic costs. For example, sea lions foraging near the bottom expend more energy than when feeding near the surface (Costa, 2008). The bulk filter feeding behavior of Balaenopterid whales is also quite costly (Goldbogen et al., 2012), requiring acceleration to high speeds, inflation of the accordian-like buccal cavity, and engulfment and filtration of massive volumes of water. To power the "largest biomechanical event on Earth," the whale creates exceptional drag forces. In contrast, deep-diving elephant seals engage in inexpensive foraging behaviors, using suction feeding to capture many small, individual fishes and squids (Naito et al. 2013).
3. *Energetics of prey choice*: The amount of work, and therefore energy expenditure an animal puts into locating prey varies as a function of the prey's energy content, availability, and location both geographically and vertically. Energy content depends on both size and proximate composition (fat, carbohydrate, protein), while availability varies as a function of absolute abundance and distribution in the environment. A predator is more efficient when foraging on prey that is densely aggregated than on prey that is evenly dispersed, and marine mammals often forage in areas and at depths where prey has been concentrated as a result of oceanographic processes like eddies, fronts, and upwelling.

Sea otters provide an excellent example of the energetics of prey choice. In unexploited areas, sea otters feed on preferred prey items like clams, abalone, or sea urchins, which are large, energy-rich, and abundant, and are easy to handle, consume, and digest. Lower quality prey are not eaten, even if abundant. As the abundance and size of their preferred prey declines, otters switch to less preferred but more accessible prey like turban snails, kelp crabs, chitons, and sea stars. Sea otters specializing on certain types of prey are more efficient predators than nonspecialists. Similarly, polar bears feed predominately on ringed seals, and only eat the energy-rich blubber layer, leaving behind the lean core of the carcass. Due to its high lipid content the blubber has a per unit mass energy almost 10 times greater than that of the lean tissue of the ringed seal.

## C. Growth and Reproduction Costs

In male marine mammals, the cost of reproduction is limited to the cost of finding and maintaining access to females. Larger body size is preferred in terrestrially breeding pinnipeds since it confers an advantage in fighting and in defense of territories, and larger animals can fast longer because they have lower mass-specific metabolic rates (Costa, 1993). In terrestrially breeding species sexual dimorphism is common while for aquatic breeders, males are smaller and sexual dimorphism is reduced or, in some cases, reversed. Despite these differences, the overall costs associated with reproduction in aquatically and terrestrially breeding males is similar.

The cost of reproduction for females can be broken down into the energetic requirements of gestation and lactation. For marine

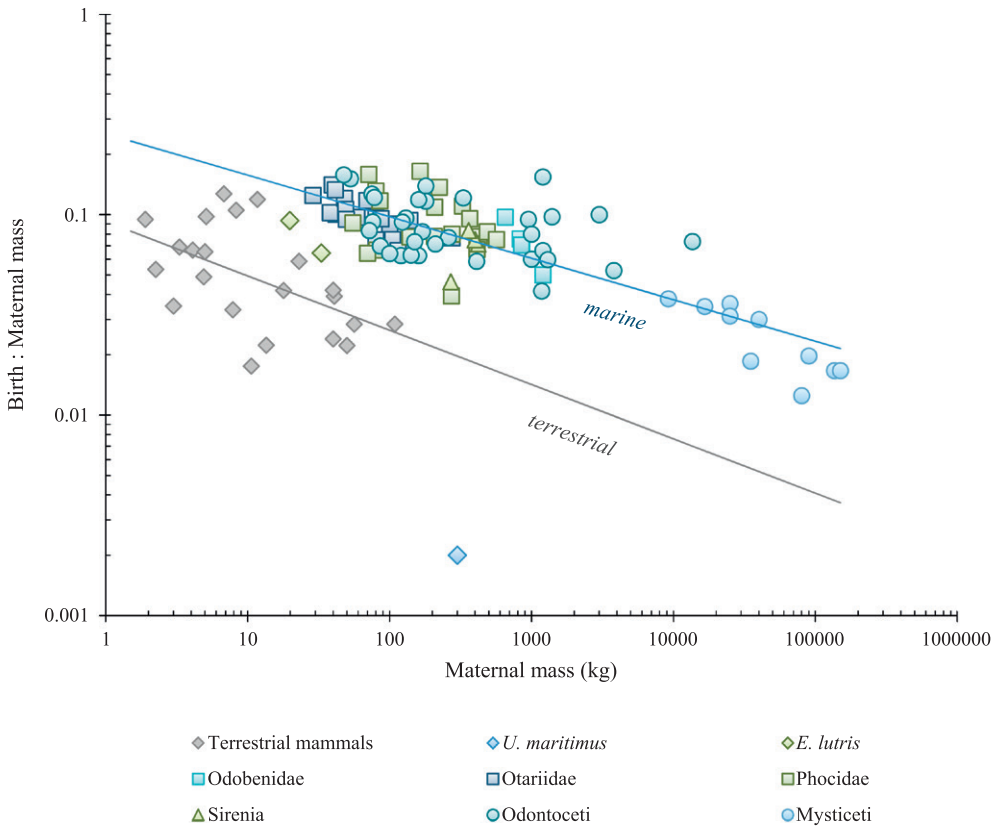


**Figure 5** *Fetal birth mass in relation to maternal mass for marine and terrestrial mammals.*

mammals, the production of precocial young that need to be capable of dealing with life in the water or on a crowded rookery within seconds of birth, requires larger fetal birth mass (and thus more energy invested in gestation) than most terrestrial mammals (Fig. 5). In contrast, marine mammals exhibit considerable variation in patterns of maternal investment during lactation. Phocid seals and mysticete whales have extremely short lactation durations (Fig. 6), which are compensated for by higher rates of energy transfer that enable the young to grow rapidly (Fig. 7). Although phocid pups are weaned early, they still rely on maternally derived energy, stored as blubber, for weeks or months after weaning. The disadvantage of this rapid growth is that most of the mass and energy is stored as fat with proportionately little protein. The advantage of longer lactation is that young get more protein and other nutrients, allowing greater growth of lean tissue; however, longer lactation is energetically more expensive (Costa, 1991, 1993).

1. *Variation in milk composition*: Most terrestrial mammals produce milk that is low in fat (e.g., 4% in cows and humans). More lipid-rich milk allows for rapid growth rates in marine mammals. For example, hooded seals produced milk that is 65% lipid, enabling a 4-day lactation interval! Lactation enables mothers to optimize the delivery of energy to their young as the energy content of milk is independent of the quality of prey consumed, or the distance or time taken to obtain it. Some species feed on fish, while others feed on crustaceans or squid, yet all produce milk with greater energy density than the prey consumed (Costa, 1991).
2. *The capital breeding strategy*: Fasting during lactation is a unique component of the life history pattern of many marine mammals. With the exception of bears, no other mammal is capable of producing milk without feeding. This strategy allows mysticetes and phocid seals to separate where and when they feed from where and when they breed, and accumulate the resources needed for lactation prior to giving birth. Upon parturition, the female fasts during lactation, provisioning young with milk derived from stored body reserves. The ability to fast during lactation is related to the amount of energy and nutrient reserves, and the rate at which they are utilized. When food resources are far from the breeding grounds, the optimal solution is to maximize the amount of energy and nutrients provided to the young while minimizing the amount of energy expended by the mother. "Metabolic overhead" refers to the amount of energy a female spends on herself while onshore (seals) or while in the calving grounds (whales). Larger females have a lower metabolic overhead than smaller females because maintenance metabolism scales as mass$^{0.75}$, and fat stores scale as mass$^{1.0}$; thus, as body size increases, energy reserves increase proportionately faster than maintenance metabolism.

Although some phocids feed during lactation, mothers typically remain on or near the rookery from parturition to weaning, and most of the maternal investment is derived from body stores. This reproductive pattern allows them time to travel and exploit distant prey, allowing the utilization of dispersed or patchy food resources, and buffers them from short-term fluctuations in prey availability (Costa, 1993). By spreading out the acquisition of prey energy required for lactation over many months at sea, northern elephant seal females only need to increase their daily food intake by 12% to cover the entire cost of

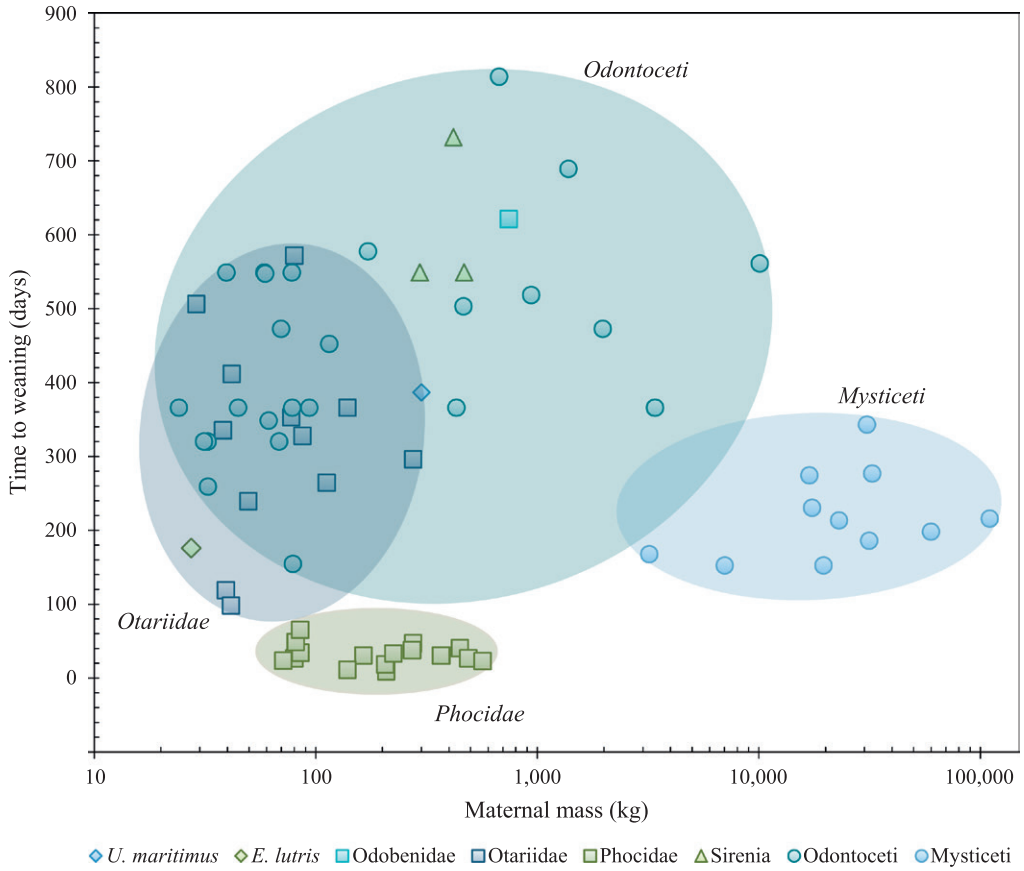


**Figure 6** *Time to weaning in relation to maternal mass for marine mammals.*

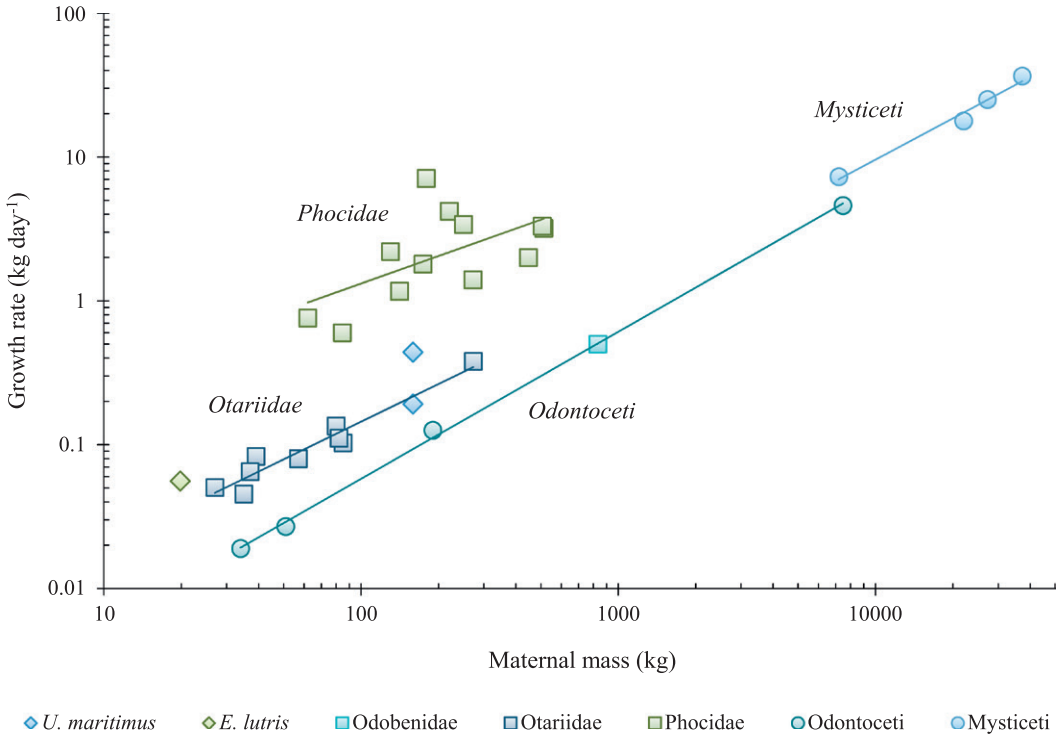


**Figure 7** *Growth rate of suckling marine mammals as a function of maternal mass. Lines represent least squares regressions for each taxonomic group.*

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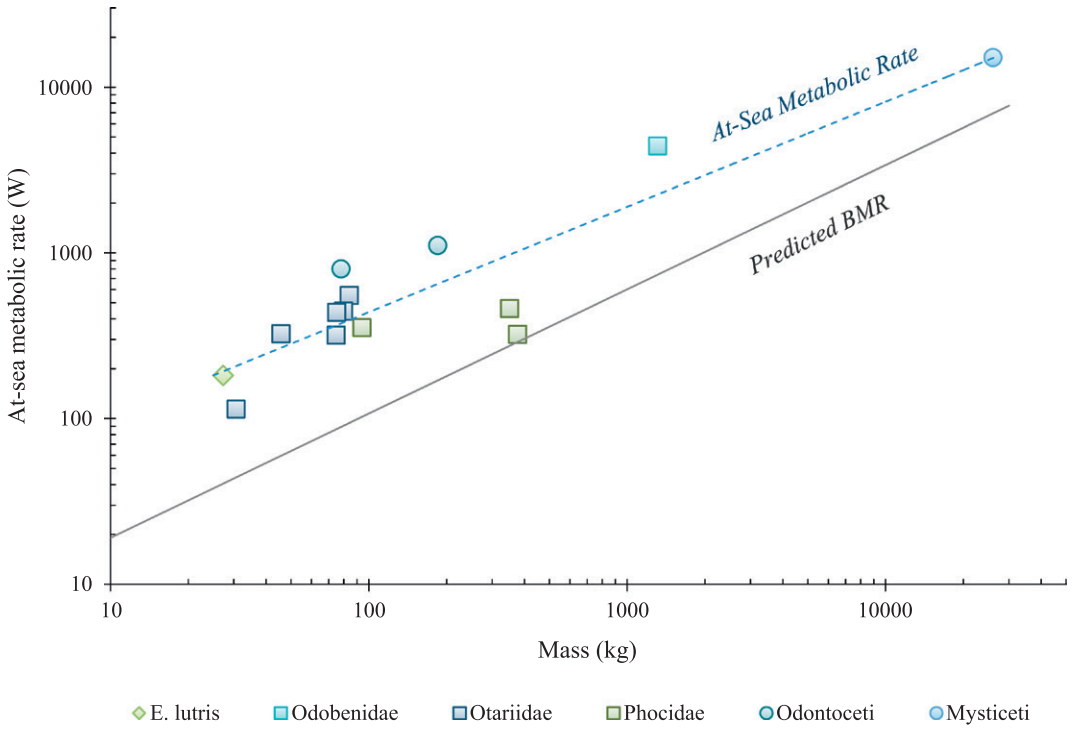


**Figure 8** *At-sea metabolic rate of marine mammals in relation to body mass. The solid line denotes the predicted BMR for equally sized terrestrial mammals; the dashed line represents the best-fit linear regression through the average of each species ($r^2 = 0.82$).*

lactation (Maresh et al. 2015). However, fasting during lactation limits the duration of investment, and the total energy that can be provided to a pup. Thus, reproductive performance (maternal investment) during a given season is indicative of the mother's foraging success over a large spatial and temporal scale. The weaning mass of a phocid pup reflects the mother's previous foraging success, whereas the subsequent postweaning survival of the pup is related to both its weaning mass (energy reserves provided by the mother) and the resources available to the pup after weaning.

3. *The income breeding strategy*: The more conventional life history pattern is to feed more or less continuously between suckling bouts. The fully aquatic groups—odontocetes, sirenians, and sea otters—alternate foraging and provisioning their young in short intervals of minutes to hours. The high metabolic rates of small, growing, dependent offspring create an additional energy burden for mothers that must be met within the constraints on dive depth and duration placed on them by the presence of their physiologically underdeveloped young. For sea otters this added energy burden is particularly extreme: high lactation costs superimposed on inherently high metabolic rates results in "end lactation syndrome," where poor body condition and increased mortality is common for mothers near the time of weaning (Thometz et al., 2014). As the smallest of marine mammals, sea otters cannot maintain large energy reserves, and are particularly vulnerable to caloric insufficiency during lactation.

As terrestrial breeders, otariid mothers alternate foraging at sea with provisioning of their pup onshore over a period of days to weeks, modifying the timing to optimize energy delivery to their young (Trillmich and Weissing, 2006). Otariid mothers making short feeding trips provide their pups with less milk energy than mothers that make long trips, but are able to feed their pups more often. This reproductive pattern requires a predictable prey resource that is located relatively near the rookery (Costa, 1993).

## D. Field Metabolic Rates

Field metabolic rate (FMR) measures an animal's total energy expenditure after all constituent costs are supported, and provides insight into the energetic strategies used by marine mammals (Costa, 2008). A number of approaches have been used to study the FMR of animals at sea and onshore. Time–budget analysis sums the daily metabolic costs associated with various activities. Other methods rely on predictive relationships between FMR and physiological variables such as heart rate or ventilation rate, between FMR and changes in body mass and composition, or between FMR and biomechanical power. For example, animal-borne accelerometers have been used to measure flipper stroking frequency and dynamic body acceleration, metrics for swim effort that should correlate with FMR (Williams and Maresh, 2016).

The best data exist for pinnipeds and the common bottlenose dolphin (Fig. 8), and indicate that foraging otariids and bottlenose dolphins expend energy at six times the predicted basal metabolic level (Costa and Williams, 2000). In contrast, the metabolic rates of diving elephant and Weddell seals are only 1.5–3 times the predicted basal rate (Maresh et al., 2015), contributing to their superb diving ability. The importance of the thermal environment for FMR can also be seen in Galapagos fur seals and sea lions, which, due to the warm equatorial climate, have a substantially reduced FMR compared to other otariids. An interesting consequence of the high FMR of some marine mammals is that the presence of a few foraging individuals can have a significant impact on community structure (Estes et al., 2016).

FMRs are quite variable both between and within species (Fig. 8), and are likely associated with year-to-year changes in both the abundance and availability of prey (Costa, 2008). For example, in response to reduced prey availability, fur seal and sea lion mothers increase their foraging effort in attempts to keep the duration of their foraging trips the same. However, there reaches a point where they can no longer increase their foraging effort and have to spend more time at sea to obtain the same amount of prey energy. If a mother spends more time to deliver the same amount of energy, the offspring receives less overall energy. As a result, more of the offspring's energy is spent on maintenance and its growth will slow. In the worst case the pup will eventually die.

### E. Disturbance Costs

As energy flow models integrate foraging success, foraging costs, and reproductive output, they can be used to assess the potential effects of an environmental or anthropogenic disturbance on individuals and populations (New et al., 2014). This approach assumes that animals respond to a disturbance by reducing or ceasing foraging, or by increasing foraging effort to make up for reductions in prey availability. In either case, the amount of energy available for reproduction is reduced and may reduce weaning mass, survival of the offspring, or survival of the mother. As marine mammals are long-lived they have the ability to reproduce over many years, making any given reproductive event less important, giving them some ability to adapt to environmental perturbations, natural or human-induced. Nevertheless, the ability of a particular species and/or life history pattern to compensate for disturbance is likely to be quite variable as some species may already be operating at or near their maximum capability. For example, due to their small size and high metabolic rates, sea otters and harbor porpoises are likely operating at the knife's edge of survival (Thometz et al., 2014), and are likely to be more sensitive to disturbance. As reproductive success is tightly coupled with local prey abundance in income breeders, they are likely to be more sensitive to disturbance and localized environmental changes compared to capital breeders, for whom reproductive success and local food availability are uncoupled. Regardless, significant alterations in trip duration, body condition, fecundity, pup growth rate, and pup survival have been observed for both income and capital breeders in response to reductions in prey availability associated with oceanographic perturbations such as El Niño. Observations such as these are providing insight into the physiological mechanisms underscoring the disparate abilities of marine mammals to adapt to increasing human use of the marine environment as well as global climate change.

## *See Also the Following Articles*

Cetacean Physiology ■ Diving Physiology ■ Pinniped Physiology ■ Swimming ■ Thermoregulation

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